

STUDIES OF TEMPORAL FREQUENCY ADAPTATION IN VISUAL CONTRAST SENSITIVITY

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SUMMARY

1. A short adaptation to sinusoidal flicker produces a temporary elevation in the temporal contrast threshold of a human observer.

2. The frequency specificity of this adaptation effect is much less than that observed with adaptation to spatial frequencies; thus it does not seem warranted to postulate the existence of distinct channels for the detection of specific temporal frequencies, as has been done in the case of spatial frequencies (Blakemore & Campbell, 1969).

3. At low frequencies, a substantial adapting modulation is necessary to produce an effect, but at high frequencies an effect can be seen even with adaptation which is below threshold (as determined by the method of adjustment).

4. This subthreshold adaptation appears to explain the observation that thresholds set by the method of adjustment rise by as much as a factor of two during the first minute of exposure.

5. No interocular transfer of the adaptation effect was observed.

6. Adaptation first appears at mesopic luminances, but its appearance is not dependent on the change from rod to cone vision. Under several conditions, however, the first appearance of flicker adaptation did coincide with a change in the deLange curve, which is attributable to the appearance of the antagonistic surround of visual receptive fields. Thus it was hypothesized that the surround is essential for adaptation.

INTRODUCTION

Recently Blakemore & Campbell (1969) have shown that the human visual system can be adapted to specific spatial frequencies. When an observer is exposed to a sinusoidal grating of high modulation for about 1 min, his spatial contrast threshold is elevated by as much as $\frac{1}{2}$ log. unit for a period of 30 sec. It is found that the adaptation is sharply specific to the frequency and orientation of the adapting stimulus. Because of the

recent interest in similarities between spatial and temporal contrast sensitivity phenomena, it seemed worth while to investigate the possibility of a similar adapting effect with temporal, rather than spatial, frequencies. Such an effect was, indeed, found, and some of its properties were studied to try to learn something of its physiological basis, and to try to use these properties to elucidate other aspects of the visual process.

METHODS

The equipment used was a simple, 2-channel, Maxwellian view system. A tungsten source (C.T. 2600° K) produced the stimulus, which was a 10° uniform field at 30 cd/m². The central 3° of this field was illuminated separately (at the same mean luminance), and could be luminance-modulated. This modulation was accomplished by a pair of crossed polaroids; one being stationary and the other attached to an oscillating D'Arsonval movement. The movement was driven by a sinusoidal signal, the amplitude of which was adjustable by the subject, using a potentiometer.

The subject's setting of the modulation was continually monitored, as a function of time, by a chart recorder. For some experiments, the subject was instructed to move the potentiometer setting back and forth continually, bracketing the threshold. The resultant plot (e.g. Fig. 5) displays the threshold as a function of time, and the magnitude of the excursions are an indication of the accuracy of the measurement. For other purposes, the subject made only a single threshold setting, which was automatically recorded as a point on the chart. The experiments described were carried out over a period of 18 months, using three emmetropic subjects, the author (R.S.), a colleague (W.R.), and a naive observer (M.A.). Except as noted, no substantial differences were observed among the various subjects.

APPARATUS

The Maxwellian view system used in the first set of experiments is shown in Fig. 1. The light beam emerges from the 2 mm aperture (A_1) and is collimated by lens L_1 . For convenience in modulating the light, the beam is focused again at aperture A_2 . Adjacent to A_2 is a circular neutral density wedge (ND), which was used to adjust the intensity of the beam. P_1 is a small piece of polarized acetate (Polaroid HN 32) which is mounted on the rotating arm of a D'Arsonval recorder-pen movement. P_2 is a stationary polarizer. Part of the modulated light beam is deflected by the beam-splitter (BS) and enters the photomultiplier (PM) where it is monitored on an oscilloscope. Finally Lens L_5 focuses the beam in a 2 mm spot on the observer's pupil. All the lenses have a 16 mm focal length. The unmodulated background is a collimated beam from light S_2 , which is brought into the optical path by reflexion on a thin glass plate (M_2). The stimuli which are seen by the observer (STIM₁ and

STIM₂) are standard 2 in. × 2 in. slides. In this experiment, the modulated stimulus is a bright spot, 3° in diameter, the edges of which are blurred to a width of about ½°. The steady background is the complement of the stimulus – a bright field with a 3° black spot whose edges were also blurred. Thus the composite of the background and the unmodulated stimulus is a uniform field.

For the experiment on interocular transfer, it is necessary to provide separately adjustable flickering stimuli for each eye. To accomplish this, a device is placed between L₅ and the observer. This device splits the converging beam into two separate beams and directs these into the two eyes (see insert, Fig. 1). The additional

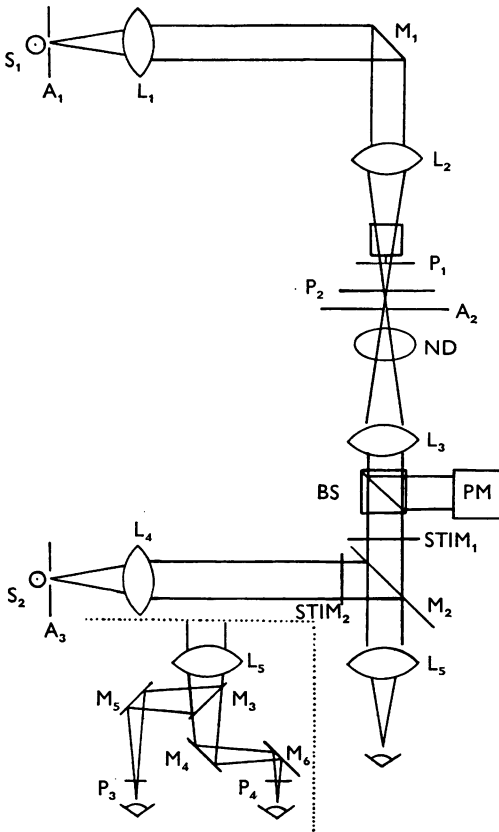


Fig. 1. The Maxwellian view system (see text for description).

flickering stimulus is produced by a second optical channel, identical to that part of the first which is between L₂ and L₃. This channel enters the optical path through the unused fourth side of the beam-splitter. This second beam is polarized in a direction perpendicular to the polarization of the first. When the combined beam is again split, after passing through L₅, a pair of crossed polarizers (P₃, P₄) separates the two channels, so that each can be seen by only one eye.

The light modulation system was designed especially for this experiment, and is considerably simpler than the Kerr-cell modulators which are commonly used. The system consists of two polarizers, one of which is attached to the arm of a rotating

D'Arsonval movement (Schwarzer no. BV 265). The two polarizers are oriented at about 30° from the crossed position. For small rotations of the movable polarizer, the change in light transmittance is linearly proportional to rotation angle. In practice, this linearity holds for modulations up to about 40%. The extent of linearity can be seen in Figs. 2, 3, 4. The system displays only a 20% loss in amplitude at 50 c/s, which is the upper limit of visual frequencies. The phase also shows only a slight lag at these frequencies, with a resonant frequency near 250 c/s.

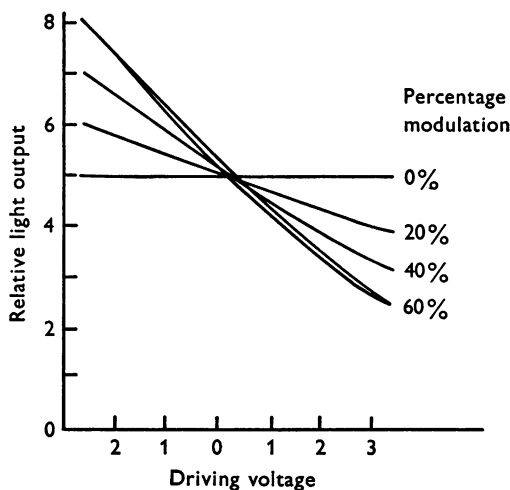


Fig. 2. Distortion in the light modulator. Lissajous figures of light output versus sine wave input for four different modulations.

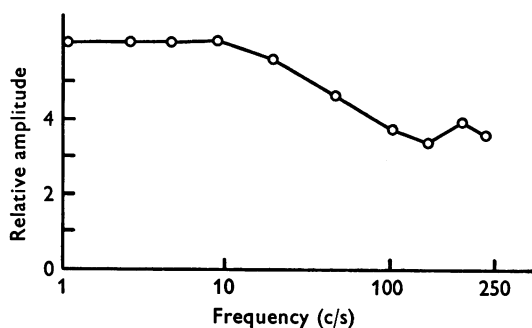


Fig. 3. Modulation transfer function of the light modulator - amplitude. The amplitude component of the MTF of the Schwartzner pen movement used as a light modulator.

The sinusoidal signal was produced by a H-P no. 203A audio oscillator. The output of this oscillator was voltage divided by a Bourne no. 3535 1% logarithmic potentiometer, ganged in a 1% linear potentiometer. The linear potentiometer drove the y axis of a H-P no. 135M X-Y recorder. Thus thresholds could be recorded directly on logarithmic graph paper. A switching network permitted the experimenter to select a variety of preset stimuli, in addition to setting of the precision potentiometer.

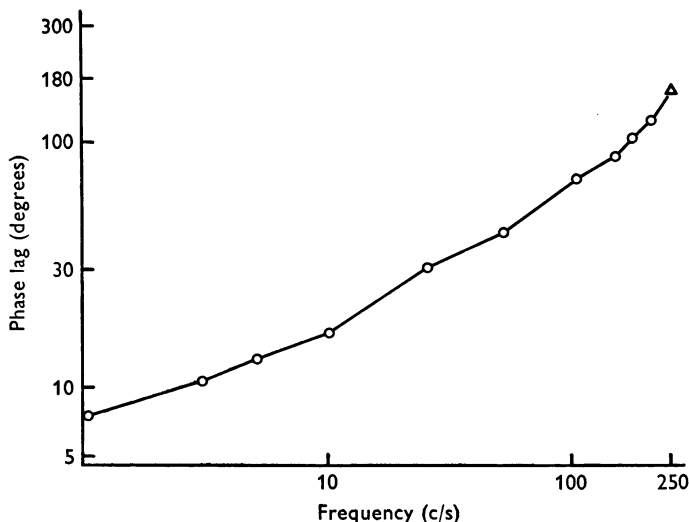


Fig. 4. Modulation transfer function of the light modulator - phase (same as Fig. 18 phase component).

RESULTS

Temporal adaptation

Preliminary observations

The presence of an adaptation effect is indicated in Fig. 5, which shows two records of threshold versus time for flicker at 15 c/s. The first record was made after fixating an unmodulated stimulus, the second after fixating a highly modulated one. In the second case, the threshold is initially elevated by about a factor of three, and slowly returns to its normal level. This basic observation has been repeated many times, with differing parameters, and comparable results are invariably obtained. Clearly some sort of adaptation effect is present; it now remains to determine some of its properties.

In order to do any further experimentation, it is useful to know how long an adaptation period and how great an adapting modulation are necessary to produce an effect. The effect of increased exposure time is shown in Fig. 6, where adapting effect is plotted against adaptation time.

The ratio of the threshold immediately after adaptation to the unadapted threshold is taken as the measure of the adapting effect. Each point represents the mean of four settings. It was found to be important that the data were taken in random order, since the threshold tended to rise slightly during the session. It is clear from the Figure that adaptation

is essentially complete after 30 sec of exposure. Pilot data at other modulations also support this conclusion, so 30 sec was adopted as the standard period of adaptation. With this knowledge, it is possible to devise a more efficient procedure for measuring adaptation than that shown in Fig. 5. In this procedure, the subject is first given a 30 sec adaptation, which is

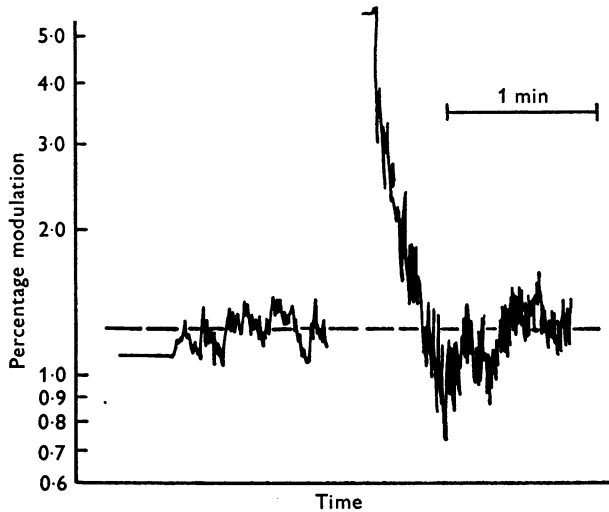


Fig. 5. Temporal adaptation at 15 c/s. Subject M.A. The left-hand trace shows the threshold after 1 min of fixating an unmodulated test spot; the right-hand trace shows the threshold after fixating for 1 min a spot flickering at 50% modulation.

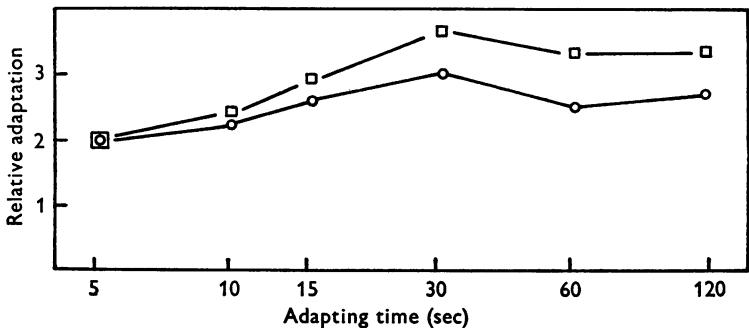


Fig. 6. Adaptation versus adapting time. Subject R.S. The amount of adaptation at 5 c/s (○) and 15 c/s (□) for a modulation of 50%, as a function of adapting time.

followed by a period of 4 sec in which he attempts to set his threshold. If he succeeds, he presses a button and the threshold is recorded as a point by the X-Y plotter. The 4 sec test period is followed cyclically by 10 sec re-adaptation periods and 4 sec test periods, until four successful settings

are recorded. This is not a particularly difficult task; typically only six test periods are necessary to achieve the four settings. This procedure is used for all subsequent experiments, unless otherwise noted.

A possible artifact in the above procedure for measuring thresholds rapidly is that the subject might inadvertently set his threshold for the perception of the pseudoflash, rather than the flicker itself. The pseudoflash is a visual transient which accompanies the onset of high-frequency flicker. Its threshold is typically lower than that of the flicker. To guard against this possibility, the subject was warned to ignore any 'transient' which might occur as the flicker was turned on, and to look instead for

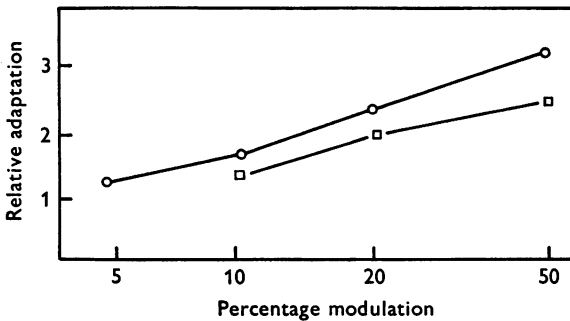


Fig. 7. Adaptation versus adapting modulation. Subject W.R. The amount of adaptation at 5 c/s (○) and 15 c/s (□) for an adapting time for 30 sec, as a function of adapting modulation.

'real flicker'. Fortunately, the threshold (deLange) characteristics for the pseudoflash and for flicker are grossly different; a measurement of the subject's deLange characteristic, using the above procedure, clearly eliminated the possibility that he was using the pseudoflash in setting his threshold.

The effect of different adapting modulations on the amount of adaptation is shown in Fig. 7. The adaptation is seen to increase monotonically with adapting modulation, with no indication that the effect saturates at high modulations. This differs from the results of Blakemore & Campbell, who found that spatial frequency adaptation saturated about 1.5 log. units above threshold. Since there is no clearly preferred adapting modulation, 50% was chosen as a convenient standard for most of the following work.

One of the most interesting results of Blakemore's study is the finding that adaptation to spatial frequencies is sharply tuned to the adapting frequency. One would like to ask, then, if a similar phenomenon can be found with temporal adaptation. The experiment to measure the frequency specificity (or band width) of the adapting effect is done by adapting at one frequency and testing at different frequencies. The results of such

an experiment, obtained from two observers, are shown in Fig. 8. It is clear from this Figure that flicker adaptation does display a frequency specificity. The effect is greatest at the 15 c/s adapting frequency (arrow), and falls off on either side of this frequency. However, compared with the findings of Blakemore & Campbell (obtained with spatial frequencies), the adaptation is not very sharply tuned. This lack of specificity was somewhat surprising, and a number of pilot studies were conducted to see if a different combination of frequency, luminance, adapting modulation, and adapting

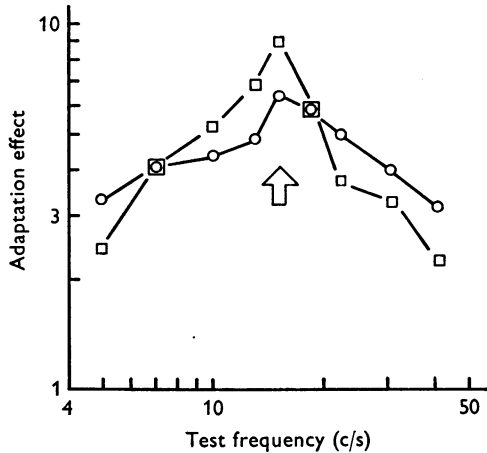


Fig. 8. Frequency specificity of adaptation. Subjects M.A. (○) and W.R. (□). The change in threshold at different test frequencies after adaptation at 15 c/s.

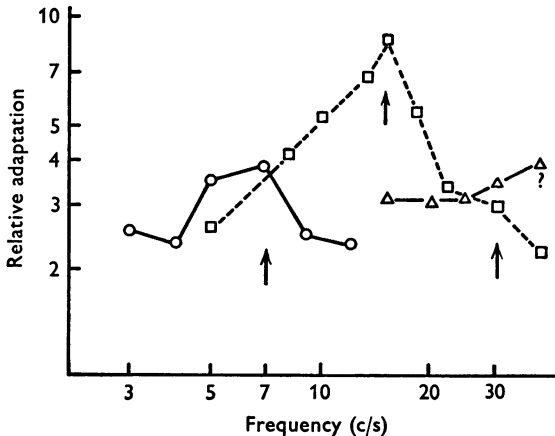


Fig. 9. Specificity at different adapting frequencies. Subject W.R. Similar to Fig. 4, for adapting frequencies of 7 c/s (○), 15 c/s (□), and 30 c/s (△). One point (marked ?) had an adapted threshold of about 80%, which is beyond the capability of the apparatus to produce an undistorted sinusoidal stimulus.

time might give different results. Specificity curves for different adapting frequencies are shown in Fig. 5. No arrangement could be found which gave a substantially sharper specificity.

Subthreshold adaptation

In the course of these experiments, an unexpected observation was made. If the flickering stimulus was set for a high frequency, and the subject asked to track his threshold, starting with the onset of flicker, it was found that the threshold rose by as much as a factor of 2 over the period of 1 min (see Fig. 10*a*). This phenomenon can first be observed at frequencies between 10 and 30 c/s (depending on the observer), and becomes progressively larger at higher frequencies. To explain this, consider the hypothesis that this 'creeping threshold' is due to temporal

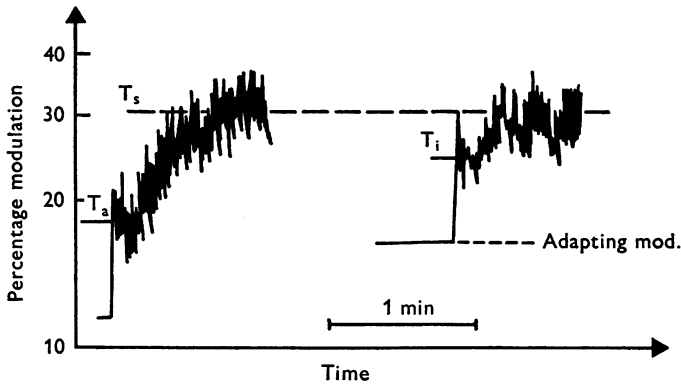


Fig. 10. *a*. Creeping threshold. Subject M.A. The progressive increase in threshold at 45 c/s after the onset of flicker. *b*. Subthreshold adaptation. Subject M.A. An initial subthreshold exposure raises the threshold immediately following (T_i) by 50% compared to Fig. 10*a*.

adaptation by the threshold stimulus itself. At first sight it seems an unlikely assumption that a threshold signal could produce a substantial change in the state of the visual system. It is shown in Fig. 10*b*, however, that an alteration in threshold can be produced even by a *subthreshold* signal. In this record (taken a few minutes after Fig. 10*a*) a subthreshold exposure is seen to have raised the initial setting of the threshold (labelled T_i) by about 50%. If this is so, then it must be the case that threshold signals can have a significant adapting effect. It is important to note, however, that the asymptotic value which the threshold approaches in time (labelled T_s) is unchanged by the pre-adaptation. Some earlier observations of similar subthreshold effects are found in Alpern & Sugiyama (1961), Akos & Akos (1968), or Rey & Rey (1965).

Before proceeding it is useful to define some nomenclature. The threshold observed immediately after adaptation will be called the initial threshold (T_i). The initial threshold observed after adaptation to an *unmodulated* stimulus is the absolute threshold (T_a), since it seems to represent the most sensitive (i.e. unadapted) state. Finally, the value of threshold which is reached after a long period of adjustment is the steady-state threshold (T_s).

Now consider what is happening in Fig. 10*a*. When the flicker begins, the system is unadapted, and threshold is low (T_a). As adaptation takes place, the threshold rises, and the observer (who is tracking his threshold)

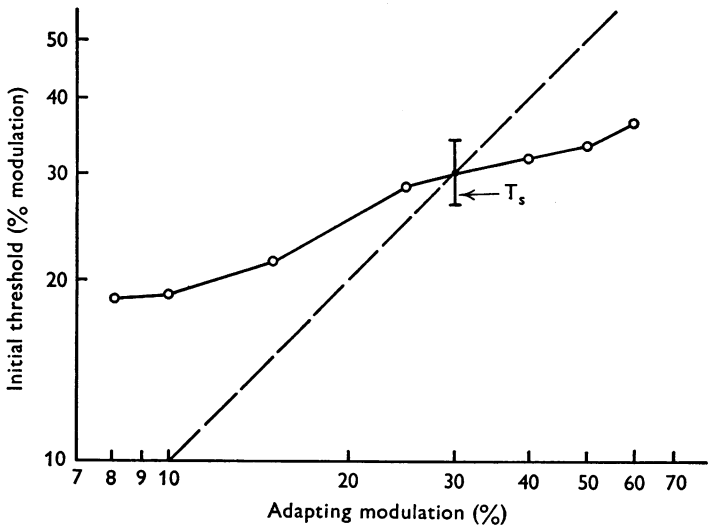


Fig. 11. Adapting modulation versus initial threshold at 45 c/s. Subject M.A. (see text).

raises the modulation. This produces more adaptation, a further rise in threshold, etc. Eventually the process levels off at the steady-state threshold (T_s). Thus the steady-state threshold can be characterized as that level of modulation which produces an adapted state such that it is, itself, at threshold. If we consider the initial threshold to be a good measure of the sensitivity of the system when adapted to a given modulation, then the above statement can be rephrased; the steady-state threshold is that modulation which equals its own initial threshold.

This is now a testable statement; it is only necessary to measure the initial threshold (T_i) for different adapting modulations and determine whether the adapting modulation equals T_i for the value of the steady-state threshold (T_s). Fig. 11 shows a plot of T_i versus adapting modulation at a frequency of 45 c/s. The dashed line is the locus of points such that T_i

equals the adapting modulation. The value of T_s was independently measured as the average of five settings by the method of adjustment, and is plotted on the dashed line. It coincides closely with the intersection of the dashed line and the plot of T_i , as predicted by the hypothesis. Fig. 12 shows three more such curves, taken at different frequencies. Again the agreement is quite close. Thus, it seems safe to conclude that the threshold, as actually measured, involves a substantial component of adaptation, produced by the test stimulus itself. Since the visual system is not normally

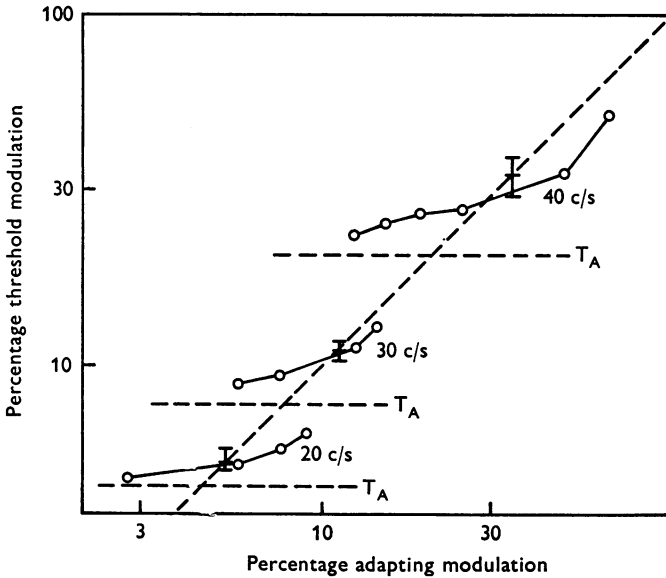


Fig. 12. Similar to Fig. 11, for subject R.S., using three different frequencies.

in an adapted state, this might be considered an artifact in the measurement of contrast sensitivity. The magnitude of this artifact can be seen in Fig. 13, which plots the MTF using both T_s and T_a . Because of the steepness of the high frequency portion of this curve, the effect appears small, but at some frequencies the difference in threshold may exceed a factor of 2. Note that the effect is not found at frequencies below about 20 c/s. The other subjects differed considerably in the lowest frequency at which this artifact could be observed. W.R. showed subthreshold adaptation even at 10 c/s, while M.A. showed no effect below about 30 c/s.

Earlier in this section, the observation was made that an observable adaptation could be produced by a subthreshold modulation. This is a sufficiently startling result that it seems desirable to investigate it further. In particular, it would be significant if a truly imperceptible stimulus could be shown to have a perceptible effect. However, a formid-

able logical difficulty is to decide on a meaningful criterion for the perceptibility of the adapting stimulus. If subjective report is the criterion, then the results are as follows. For adapting modulations above T_s , the adapting signal is always seen. For modulations between T_s and T_a , the modulation is seen at first, and then fades away. Modulations below T_a are not seen. These results agree nicely with the explanation of the creeping threshold. However, subjective report is not a very sensitive criterion. Typically an observer will show a much lower threshold with more refined psychophysical techniques. For this reason, the method of successive matched pairs was

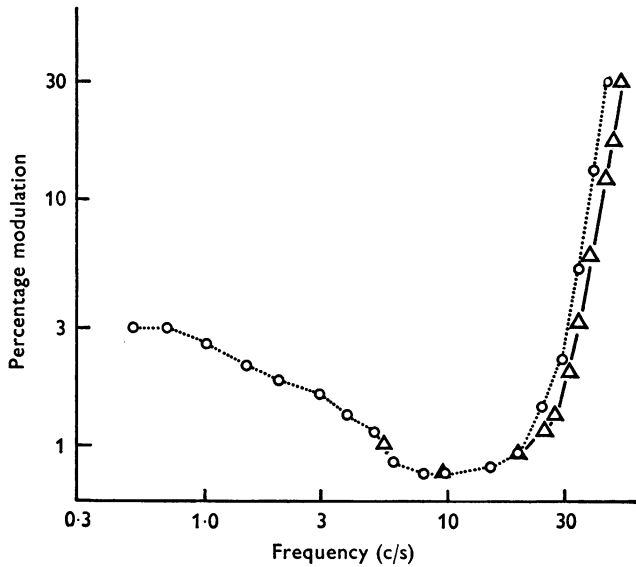


Fig. 13. The adaptation artifact. Subject R.S. The absolute threshold (Δ) and steady state (\circ) as a function of frequency.

used to determine the threshold at 45 c/s, under the same conditions as in Fig. 8. The subject was presented with fifty-four pairs of stimuli, each 2 sec long, and required to indicate which of the pair was flickering. The results (Fig. 14) show that the subject reached chance performance at a modulation of about 0.06. Subthreshold adaptation was immediately measured at this modulation, but the effect was not significant ($P = 0.1$, t test, 1-tailed). Adaptation was clearly present at an adapting modulation of 0.08, however. Thus there does not seem to be any basis for asserting that an adapting effect can be produced by an imperceptible signal. Rather, adaptation disappears concurrently with perception, as measured by the most sensitive psychophysical tests.

Temporal adaptation and other visual phenomena
Interocular transfer

It would be desirable to try to relate temporal adaptation to other known aspects of visual physiology and to suggest an anatomical locus for the effect. One of the simplest psychophysical experiments which can be done to localize the site of a visual effect is to determine whether the effect transfers interocularly. In this case, an unexpected artifact intruded itself. The experiments thus far described have all used a Maxwellian view system for the right eye. In order to do an interocular transfer experiment, it would be necessary to switch eyes in front of the single eyepiece. Such a procedure would leave the tested eye in the dark during the 30 sec

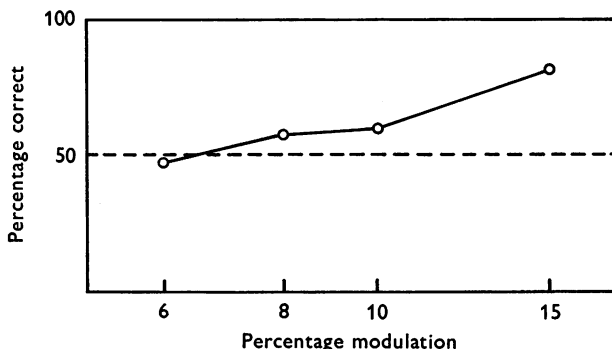


Fig. 14. Detectability at 45 c/s. Subject M.A. Percentage correct responses to successive matched pairs as a function of modulation.

adapting period. Unfortunately, a short period of dark adaptation is, in itself, sufficient to produce a change in threshold similar to that produced by adaptation. To avoid this artifact, an adaptor for dichoptic stimulation was fitted to the Maxwellian view system. Provided with the adaptor, each eye saw a stimulus essentially similar to the one used for all the preceding studies, but the stimuli presented to the two eyes could be varied independently (see Appendix). Thus, while the left eye was adapting, the right eye perceived a uniform field. When the adapting modulation disappeared, flicker appeared in the right eye, and the subject set his threshold. Three subjects were used, and none showed any apparent transfer. Fig. 15 shows the results of R.S. The left-hand record shows 30 sec of adaptation at 50% modulation delivered to the left eye (the level line) followed immediately by a measurement of the threshold of the right eye; no adaptation is apparent. The second record is a control: 30 sec of no adaptation, followed by a measurement of the threshold of the right eye; it is not apparently different from the first record. The third record is normal monocular

adaptation: adaptation of the right eye, followed by a test of the right eye; there is a normal adaptation effect. The other subjects yielded similar results; except that W.R. (Fig. 16) had a transient interocular change of threshold lasting about 30 sec. He attributed this to binocular rivalry, but in any case, its time course was grossly different from that of temporal

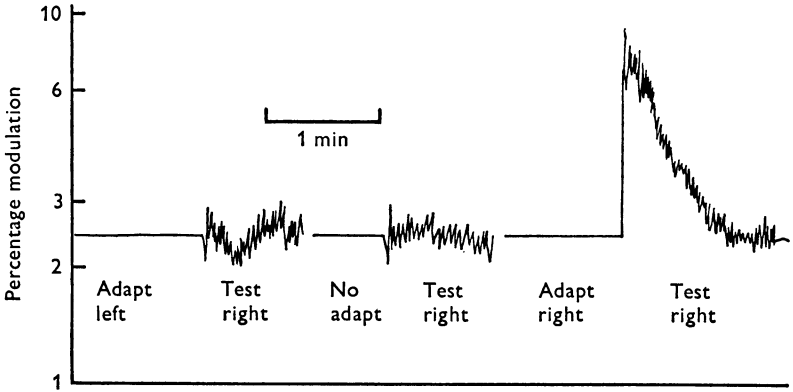


Fig. 15. Interocular transfer at 10 c/s. Subject R.S. The traces show threshold for the right eye after: adaptation of the left eye, no adaptation, and adaptation of the right eye, respectively.

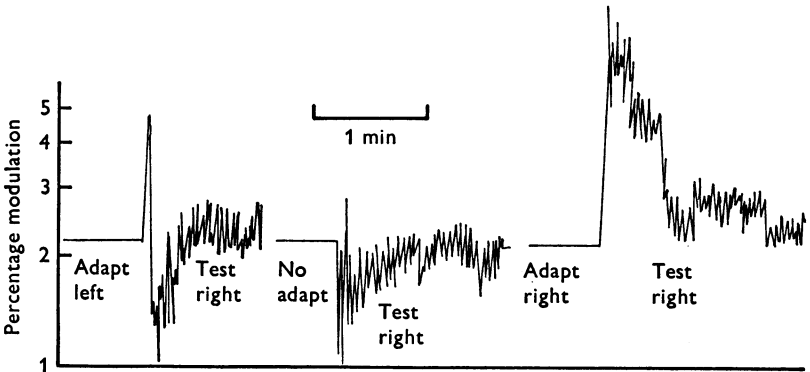


Fig. 16. Interocular transfer at 10 c/s. Subject W.R. Similar to Fig. 15 for subject W.R. This subject showed a slight decrease in threshold with interocular stimulation (see text).

adaptation. Thus, it seems safe to conclude that dichoptic transfer is either absent or very slight. This suggests that temporal adaptation is a relatively peripheral phenomenon, presumably occurring before the site of binocular interaction.

Anatomically, this result seems to imply a subcortical site for adaptation. However, it is conceivable that the site is in the monocular cells of

the striate cortex. There is some evidence that a concentration of such units exists around the termination of the optic radiation in layer 4 (Hubel & Wiesel, 1969). To check this possibility, the author conducted pilot experiments to see if adaptation with a flickering grating was specific to the orientation of the adapting grating, as would be expected if orientation-specific units were being adapted. Although the results were not entirely conclusive, it appears that there is little, if any, specificity. Thus it seems unlikely that cortical neurones (all of which are believed to be orientation-specific) are being adapted.

Adaptation at mesopic luminances

The visual system is often thought of as consisting of two independent parts, the scotopic and photopic systems. Is temporal adaptation specific to one of these systems? To study this question, the apparatus was altered slightly, so as to provide a stimulus maximally effective for stimulating scotopic vision. Using a Wratten no. 95 filter, the white light was reduced to a narrow band around 490 nm (the peak of scotopic sensitivity) and the subject was instructed to view the edge of the field, so that the stimulus fell on the rod-rich area, 5° from the fovea. With this arrangement, there is a range of about 2 log. units of luminance (0.005–0.5 scotopic td) over which the stimulus appears achromatic but flicker thresholds can still be measured. Fig. 17 shows records of the subject tracking his threshold after adaptation at different luminances. During the initial level portion of each record, the subject received 30 sec adaptation at 4 c/s, with a modulation of 0.5; immediately thereafter he tracked his threshold. The first hint of an adaptation effect is at a luminance of 0.5 scotopic td, which is also the luminance at which colour appears. Both colour and adaptation are quite clear at 1 td. The converse of this experiment was also attempted; that is, adaptation was measured in the isolated red cone system. A Wratten no. 92 filter produced a stimulus with a wave-length near 645 nm, and the subject viewed a 1° stimulus, directly on the fovea. There is no luminance which is achromatic here, and no luminance at which adaptation is not found. (This is subject to the obvious reservation that it is always hard to demonstrate adaptation when the threshold modulation approaches the highest available adapting modulation. In fact, the lowest luminance used had a threshold of about 40%.)

These results seem to indicate that temporal adaptation is purely a photopic phenomenon: further study, however, suggests the problem is more complicated. If the adaptation is specific to cone vision, it is likely that adapting one of the three cone systems will have no effect on the other two. This hypothesis is immediately testable and can be rejected. Adapting with a deep red stimulus (645 nm) produces about as much adaptation

effect on a blue test stimulus (440 nm) of equal brightness as does the blue stimulus itself, and vice versa. While a careful parametric study might reveal subtle effects of chromatic transfer, the hypothesis that adaptation is specific to a particular cone system is certainly false.

Possibly the observation that temporal adaptation appears at the same luminance as colour was purely coincidental, and that the appearance of temporal adaptation actually depends upon the level of scotopic stimulation. This can be tested by varying the experimental conditions so as to

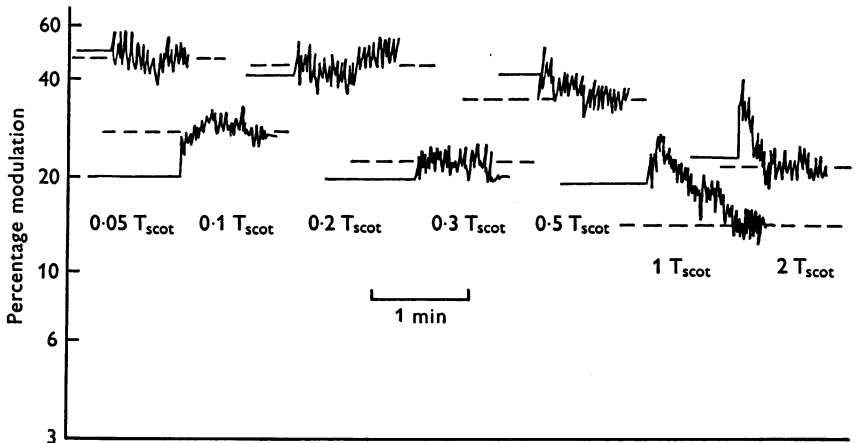


Fig. 17. Adaptation at scotopic levels. Subject R.S. Plots of threshold after 30 sec adaptation to 5 c/s at 50% modulation, for seven different retinal luminances. For compactness, alternate records have been displaced upward. Adaptation appears at about 0.5 scotopic td.

change the photopic luminance of the stimulus, without changing the scotopic luminance. If it is photopic stimulation which is important, then the amount of adaptation at low levels will change accordingly, whereas there will be no change if the level of scotopic stimulation (or some other quantity closely related thereto) is the important factor. Two methods were used to selectively change the level of photopic stimulation; the Stiles-Crawford effect and the use of two different wave-length stimuli.

The apparatus was set up for scotopic stimulation at a luminance of 1 scotopic td, as described above, and adaptation was measured, as shown in Fig. 18. The observer's eye was then moved laterally, about 3 mm, so that the beam entered at the temporal edge of the pupil. Under these conditions, the Stiles-Crawford effect should reduce light absorption by cones (and, hence, the effective photopic luminance) by about $\frac{1}{2}$ log. unit (Stiles & Crawford, 1933); absorption by rods is unaffected, however. This differential effect was reflected in the fact that the colour of the stimulus

disappeared, but the brightness, which is mainly due to rods at this luminance, was only slightly changed. If adaptation depends upon cone stimulation, then under these conditions it should largely disappear; whereas if rods are being adapted, the change should be slight. Fig. 18 shows two records of adaptation, one with the Stiles-Crawford effect, and one without. There is no apparent difference.

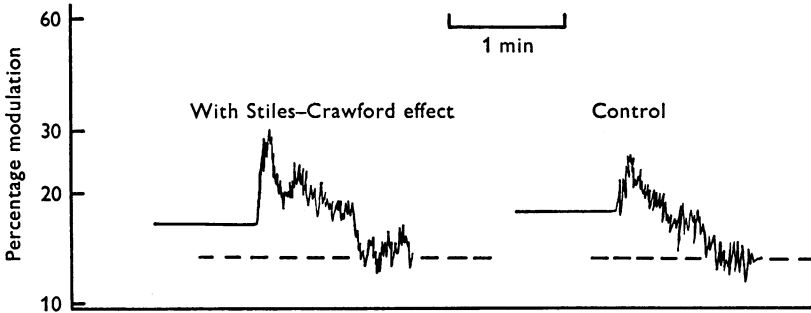


Fig. 18. Adaptation with photopic stimulation reduced by the Stiles-Crawford effect. Subject R.S. (see text).

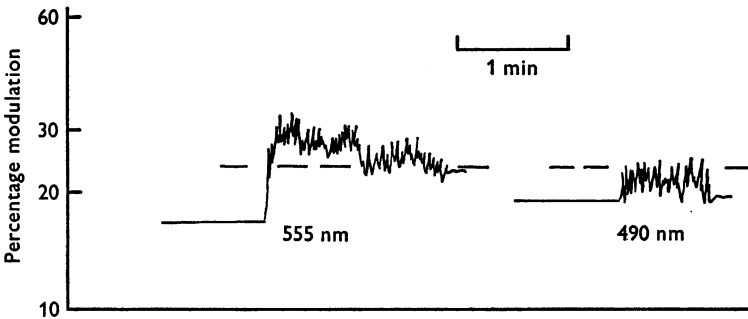


Fig. 19. Adaptation with a 555 nm stimulus. Subject R.S. (see text).

As a final test, the apparatus was set up for scotopic stimulation at a luminance of 0.3 scotopic td. At this luminance there is no apparent adapting effect (see Fig. 17). The wave-length of the test spot was now changed to 555 nm (Wratten no. 99 filter). For an equal scotopic luminance, 555 nm has ten times the photopic luminance of 490 nm. The scotopic luminance of the new test spot was equated to the old by inserting a neutral density filter which reduced the luminance of the entire field until it was achromatic, and then matching the brightness of the test spot to that of the surround. When the neutral density filter was removed, the luminance was restored to 0.3 scotopic td and the test spot now showed a faint green colour. This was to be expected, since the new stimulus is about ten times more effective for stimulating cones, though its effectiveness for rods is

unchanged. Hence, if adaptation depends upon cone stimulation, it should now appear at a luminance of about 0.05 scotopic td, ten times lower than that observed in the earlier experiment using a 490 stimulus. In fact, Fig. 19 shows that there is little, if any, adaptation at 0.3 scotopic td, yet this stimulus now has the highest photopic luminance of any stimulus used in this part of the experiment. It must be concluded, then, that temporal adaptation is not confined to either the rod or cone system, and that the initial observation that colour and adaptation appeared at the same luminance was coincidental.

DISCUSSION

Spatial and temporal adaptation

In their study of the parallel phenomenon of spatial frequency adaptation, Blakemore & Campbell (1969) lay considerable stress on the sharp frequency specificity of the adapting effect. They consider this to be support for the theory that spatial modulation is not detected by a single mechanism, but by 'functionally separate mechanisms... each responding maximally at some particular frequency and hardly at all at spatial frequencies differing by a factor of two' (Campbell & Robson, 1968). The envelope of the responses of all these mechanisms (channels) represents the familiar spatial modulation transfer function. This hypothesis implies that the separate channels have real functional significance in that the perceived size of an object depends on the relative excitation of the various channels. Blakemore & Sutton (1969) have, in fact, shown that spatial adaptation can substantially alter the perceived size of gratings and other stimuli.

It was somewhat surprising, then, to find that the specificity of temporal adaptation was very much less than that of spatial adaptation. Indeed, it seems meaningless to refer to the existence of fatiguable channels (implying separateness) when adaptation at any particular frequency has a measurable effect at all frequencies. It appears then, that the temporal portions of the visual system are not profitably described by an analysis into separate, frequency specific channels; and that such specificity as exists may be of no real functional significance.

The site of adaptation

The phenomenon of 'sub-threshold adaptation' is a most curious finding. Although careful investigation has shown that the adaptation is not truly 'sub-threshold', when very sensitive measures of detection are used, it is still remarkable that such a weak signal should produce adaptation. Commonly, effects like the motion-after-effect or spatial adaptation have been explained in terms of neuronal fatigue, a break-down in normal operation due to over-stimulation. Subthreshold adaptation does not seem

quite comparable to this type of adaptation effect. The fact that it can be observed with the faintest perceptible adapting stimuli makes the possibility of neuronal fatigue most unlikely. Rather, subthreshold adaptation resembles the negative feed-back theory of lateral inhibition suggested by Glezer (1965) or the self-inhibition in *Limulus* proposed by Stevens (1964). The essence of these theories is that the firing of even a single impulse by a neurone produces a relatively long-lasting self-inhibition. Thus the cell limits its own firing rate even at the lowest levels. These models were proposed as part of the light adaptation process. However, since flicker adaptation is observed at constant mean luminance, it seems that the site of adaptation must be at a higher visual centre, which responds only to *change* in luminance. Electrophysiological studies indicate that it is the lateral geniculate which responds most vigorously to luminance changes in unpatterned stimuli, and hardly at all to steady luminance (DeValois, Jacobs & Jones, 1962). The geniculate as a site for adaptation would be consistent with the observation that adaptation does not transfer interocularly. Certain unpublished observations of the author are also relevant here. It was noticed that cells of the lateral geniculate of cat display a response to sinusoidal flicker which decreases for at least the first 15 sec of exposure. If the modulation of the flicker is low enough, the response may actually cease. Moreover, the effect seems to be most pronounced at high frequencies. As far as these observations go, they offer a good physiological correlate for temporal adaptation. It is unfortunate that the present study had not been conceived at the time of these observations, since further neurophysiological investigation appears highly promising. An important observation (W. A. Richards & R. A. Smith, unpublished results) is that temporal adaptation displays 'reverse size-scaling' (Richards, 1968). According to Richards' theory, this excludes the retina as a possible site for the effect (see also Richards & Smith, 1969). In conclusion, then, there is a reasonable evidence, all of it indirect, however, which implicates the lateral geniculate as the site of temporal adaptation.

Adaptation and the receptive field

Thus far, adaptation has been treated as a single phenomenon. However, it is quite possible that there are separate processes involved, which are reflected in the different behaviour at high and low frequencies. Specifically, the appearance of subthreshold adaptation at high frequencies suggests that a different process may be coming into operation. It is interesting that Kelly (1961) observes a difference in threshold characteristics at high and low frequencies. At high frequencies the contrast threshold is determined entirely by the absolute amount of modulation, independent of luminance; at low frequencies the threshold depends upon relative

modulation. It is believed (Smith & Richards, 1969; Kelly, 1969) that the difference in threshold characteristics at low frequencies is due to the appearance of antagonistic interaction from the surround of visual receptive fields, while at high frequencies these interactions are not present. Possibly, then, the different behaviour of temporal adaptation at high and low frequencies also reflects this change in the interaction of the different parts of the receptive field.

If receptive field interactions are involved in temporal adaptation, then any process which affects visual organization might be expected to have an effect on adaptation as well. One such possibility is reported by Barlow, Fitzhugh & Kuffler (1957), who observed that the antagonistic surround of retinal receptive fields tends to be more prominent at high luminances and to disappear altogether at low luminances. Barlow showed that although the disappearance of the surround typically occurs at a mesopic luminance, it is a process separate from the change from rods to cones. The same implication can be drawn from single-unit recordings in the lateral geniculate (Wiesel & Hubel, 1966; Jones, 1966). It is a plausible hypothesis, then, that temporal adaptation is associated with the antagonistic surround, and is not observed at low luminances because the surround is absent. Unfortunately, electrophysiological techniques for determining receptive field organization are not available in psychophysics; however, certain characteristics of the temporal modulation transfer function are believed to directly reflect this organization. These characteristics can be used to indirectly demonstrate the desired correlation between adaptation and the presence of the surround.

In an earlier paper (Smith, 1969) the author found evidence for a progressive change in the temporal reception properties of the visual system which can be attributed to the gradual appearance of the antagonistic surround. In this study, the author was concerned with the temporal modulation transfer (deLange curve) of the scotopic visual system. It was found that at scotopic luminances the deLange curve differed from that which is seen at photopic levels in that it is completely flat at low frequencies. The photopic deLange curve always shows a pronounced peak at about 10 c/s, accompanied by a fall-off in sensitivity at lower frequencies. It was found that these photopic characteristics began to appear in the deLange curve at luminances above 0.5 scotopic td, the same luminance at which colour and temporal adaptation also appear. The question naturally arose whether this change in the deLange curve was indeed due to the action of the photopic system, as the simultaneous appearance of colour would suggest. To separate the rod and cone systems, the Stiles-Crawford effect and the use of yellow-green stimuli were employed in experiments analogous to those described at the end of the first part of this paper. The

result was that the appearance of the low-frequency fall-off of the deLange curve is essentially independent of the transition from rods to cones. Moreover, the appearance of temporal adaptation seems to parallel that of the low-frequency fall-off under all of these conditions. Thus, it seems plausible that the two phenomena are different manifestations of the same process. But, since the low-frequency fall-off in the deLange curve is believed to be due to the effect of the antagonistic surround, it is implied that there is an intimate connexion between temporal adaptation and the presence of the receptive field surround.

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